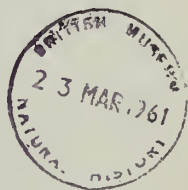


NOTES ON EOCENE TARSIOIDS
AND A REVISION OF SOME NECROLEMURINAE

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SYNOPSIS

IN this paper the problems of the relationship of European Eocene Necrolemurinae to each other and to contemporaneous and later Primates are considered. A re-affirmation of tarsioid affinities is made for this group, and it is ranked together with Tarsiinae in the family Tarsiidae. Evidence substantiating resemblances in dental formulae, tooth cusp patterns, auditory construction, and cranial osteology between tarsiines and necrolemurines is presented. *Pseudoloris* is assigned to the Necrolemurinae and the taxonomy of *Nannopithec* is revised. In conclusion, a number of dental similarities between necrolemurines, omomyids and North American anaptomorphids (as defined by Gazin, 1958) are evaluated.

ABBREVIATIONS

- A.M.N.H., American Museum of Natural History, New York
 B.M.N.H., British Museum (Natural History)
 G.P.I.H., Geological and Paleontological Institute, University of Halle-Wittenburg
 Montauban, Natural History Museum, Montauban, France
 M.C.Z., Museum of Comparative Zoology, Harvard University
 Paris, National Museum of Natural History, Paris
 P.U., Princeton University

I. *NECROLEMUR ANTIQUUS* FILHOL, AN EOCENE TARSIOID PRIMATE

The Eocene necrolemurine primate *Necrolemur antiquus*¹ from the Quercy phosphorites and possibly of early Ludian age, has long been thought to be a typical tarsioid primate. Indeed, this form has been one of the primary bases for the hypothesis that many of the small Eocene Primates of Europe and North America can correctly be called tarsioid, in that its characters link it and thereby some other Eocene Primates, in particular the necrolemurines, with the living *Tarsius*. Gregory (1915 : 30) has given some of the reasons for this placement of the group as has Simpson (1940 : 198) for *Pseudoloris*, here assigned to the necrolemurines, and the case for affinities with *Tarsius* has been most recently expressed by Gazin (1958 : 99).

In view of Hürzeler's conclusion (1948) that *Necrolemur* is a lemuroid primate the investigations presented in this paper were undertaken at the suggestion of Sir Wilfrid Le Gros Clark.

The lemuroid interpretation. Hürzeler (1946, 1948) stated that the structure of the skull of *Necrolemur* (principally the auditory region) as seen in Montauban 9, is lemuroid, and that this primate exhibited no special resemblance to *Tarsius* that could justify calling it a tarsioid. This opinion, which was in part suggested by the material examined by him, considerably affected subsequent thinking on primate taxonomy and it is advisable to consider here in some detail the construction and placement of the tympanic ring of *Necrolemur* together with the significance of this structure in the reconstruction of the phylogeny of Primates. Hill's comments (1955 : 293) are fairly typical of the reaction to Hürzeler's observations.

"Hürzeler has dissected the bulla of one specimen and finds, surprisingly, that the interior does not resemble that of *Tarsius*, but agrees rather with that in Malagasy lemurs and of *Adapis*. He disproves the conclusion of Stehlin that the annulus tympanicus (ectotympanic) is fused with the bulla, for he declares it to be quite freely suspended in the tympanic cavity. Moreover, it is not a simple ring, such as occurs in the fossil Malagasy types, but expanded into a plate-like form, attached below and laterally to the inner end of the osseous meatus."

Since Hürzeler's suggestion that *Necrolemur* is lemuroid there has been a tendency to maintain that a distinction between lemuroid and tarsioid types cannot be made among early Tertiary primate species. This view was expressed by Simpson (1955 : 438) as follows :

"The majority of Eocene genera have at one time or another been considered 'tarsioid.' Re-study of some, especially those represented by skulls or other relatively good material has resulted in their transfer to the 'lemuroids.' . . . *Nannopithecus*, *Necrolemur* and *Microchoerus* (see Hürzeler, 1948)

¹Determinations on the cranial anatomy of *Necrolemur antiquus* are facilitated by the relatively large number of skulls of this species which are available for study in the following European and North American museum collections : Basel number Q.H. 470, Montauban 9, Paris Museum (five skulls), British Museum M3747 and M4490. Museum of Comparative Zoology, Harvard University, M.C.Z. 8879, and at Princeton University, P.U. 11465. I have studied all these specimens excepting Montauban 9. Stehlin (1916) also mentioned two skulls in the collections of the Faculty of Sciences at Marseilles.

are examples particularly to the point. Still the mass of 'Anaptomorphidae' (probably not a natural family even after recent removals) has continued to be labelled 'tarsioid.' The fact is that there is no convincing evidence that any early primate is more 'tarsioid' than 'lemuroid' in natural affinities." Simpson (following Hürzeler's assignment of the necrolemurines to the Lemuroidea) was correct in suggesting that the term tarsioid was no longer meaningful. *Necrolemur* and its allies had been thought to have more resemblance to *Tarsius* than any other European or North American early Tertiary primate stock.

It is possible to question on various grounds whether the Necrolemurinae should be called tarsioids, even if one believes that the evidence for their close association with the ancestral line of *Tarsius* is sound. It is not possible, however, to assign the necrolemurines to the Lemuriformes as Piveteau (1957 : 64-71) has done while leaving all the much less *Tarsius*-like North American "anaptomorphs" ranked with the Tarsiiformes. No other early Tertiary primate is more convincingly tarsioid than *Necrolemur*.

MORPHOLOGY

Ectotympanic.—Hürzeler's view is most clearly stated (1948 : 28) in a section beginning, "Das Verhalten des Annulus tympanicus von *Necrolemur* entspricht prinzipiell jenem von *Adapis* . . .". The accompanying Plates 12 and 13, of the annulus tympanicus of *Necrolemur*, B.M.N.H. M4490 (from Mouillac, France) and Plate 14 of *Adapis parisiensis*, B.M.N.H. M1345 (from Caylux, France), are sufficient to show that these two forms have little if any significant similarity in the position and relationships of the ectotympanic element. Stehlin (1916 : 1352) also stressed this difference remarking : "Das Verhalten des Annulus tympanicus ist somit bei *Necrolemur* ein ganz anderes als bei *Adapis*". In *Adapis* the annulus lies within the bulla, it is free, and there is no bony external auditory meatus whatever in specimens examined by me. In these regards the annulus tympanicus of *Adapis* corresponds closely to the situation of this bone in the great majority, if not all, of the living members of the Lemuriformes, e.g. *Daubentonia* and *Lemur*. It would, perhaps, be tedious to recite how often the free, ring-like tympanic has been given as a character of the Lemuriformes ; van der Klaauw (1931 : 12) listed about thirty page-references to this effect for various living and fossil lemuroids (including *Adapis* and *Notharctus*). In some living prosimians, other than *Tarsius*, such as *Perodicticus* and *Lemur*, a slightly developed bony external meatus has been reported, but it is not truly tubular (see van der Klaauw, 1931 : 155-156).

Unlike any living lemur or loris, *Necrolemur* has a remarkably long bony external meatus (typically longer than that of *Tarsius*) which is fused to the bulla internally. The latter feature can clearly be determined by examination of the internal posterolateral part of the ventral bulla wall of *Necrolemur* in B.M.N.H. M4490. The conclusion that the structure applied and fused to the ventrolateral bulla wall (see Plates 12 and 13) is the inner end of an expanded and tubular annulus seems inescapable. It is not very difficult to reconcile this observation with the figures and discussion in Hürzeler (1948). I interpret the scalloped areas seen in the region of the anterointernal margin of the ventral side of the annulus of Montauban

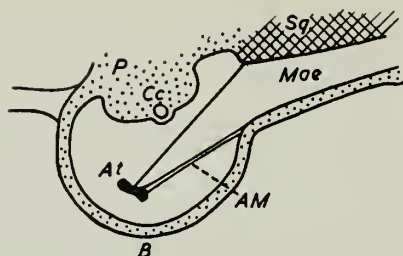


FIG. 1a Cross sectional diagram of auditory bulla of Necrolemur antiquus (after Hürzeler, 1948, fig.29.)

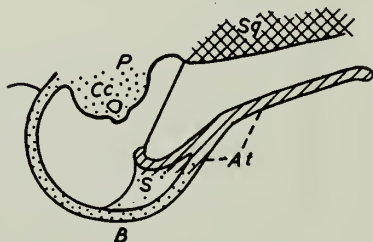


FIG. 1b Diagram of cross section of auditory bulla of Necrolemur antiquus (Brit. Mus. Nat. Hist. no. M 4490.)

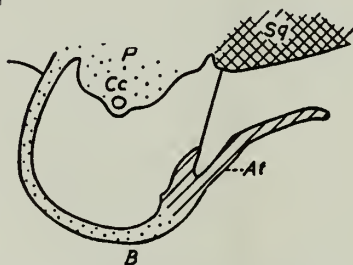


FIG. 1c Cross sectional diagram of the auditory bulla of Tarsius spectrum (Princeton Univ. ost. coll. no. 375.)

P-Petrosal *B*-Bulla *Cc*-Carotid canal *At*-Annulus tympanicus
AM-Annulus Membrane *Mae*-Ext. auditory meatus *Sq*-Squamosal
S-strut joining tympanic ring and bulla wall

9 (see his figure 27) as the bases of the struts which connect the expanded ring and bulla wall in this area. In *Necrolemur* the annulus consists of a thin lamina of bone partly fused to and partly composing the ventral wall of the bulla in the region of the internal end of the external bony meatus, turning up from the internal surface of the bulla along its mesiad margin. This internal free margin of the ring (the direct support of the tympanum) is, at intervals, further secured to the ventral bulla wall by struts (six are visible in B.M.N.H. M4490, four in M.C.Z. 8879 and one in P.U. 1165), most of which run parallel to the main axis of the bony external meatus. These struts do not occur in *Tarsius* or in any other primate described to date. Nevertheless, *Necrolemur* exhibits a real resemblance to *Tarsius* in the fusion of the ring with the bulla wall and in the lengthening of the bony meatus. In *Tarsius spectrum* a ridge projects from the inside of the ventral bulla wall running around the circumference of the ear drum upon which the tympanum is stretched. This, as in *Necrolemur*, is the internal free margin of the ring. The main difference from *Necrolemur* being that this ridge or margin is inclined more laterally.

The conformation of the annulus tympanicus suggested for *Necrolemur* is indicated in Text-fig. 1, which compares a cross-section of the auditory bulla given in Hürzeler (1948, fig. 29) with that of B.M.N.H. M-4490, and of *Tarsius spectrum*. As can be seen in Plate 13, it is possible to trace continuous bone from the left hand margin of the removed part of the bulla wall (at A) to the remaining fragment of the external bony meatus (at B). Evidently the plate-like area in the centre of this figure corresponds to the part of Montauban 9 referred to by Hürzeler as the "Annulus-Membran". This structure is clearly ossified and would appear to be more reasonably considered as part of the expanded annulus. There is clearly a continuum of bone between the internal free margin of the annulus and osseous meatus. Possibly the expanded and fused ring in the ancestry of both *Tarsius* and *Necrolemur* arose initially by a spreading of the ossification centre of the ectotympanic through the annulus membrane and outward to form a tubular meatus. Whatever the origin, the end result is very similar in these two Primates. Hill (1955 : 9) has summed up the conventional view as to the significance of an expanded tympanic ring for primate taxonomy as follows :—

"The tympanic bone [in 'haplorhine' primates] is very variable, but the specialized lemurine condition, where the annulus is enclosed within the bulla, never occurs. In tarsioids and catarrhines the ring is produced outwards in the form of a bony tube (osseous meatus), but in Platyrrhini the lorisoid condition persists, i.e. with the annulus exposed and contributing to the formation of the wall of the bulla (van Kampen, 1905)".

Hürzeler (1948 : 29) cites Lorenz von Liburnau (1905) as a source for statements about a tubular ectotympanic in *Megaladapis* but the latter's comments are vague and capable of more than one interpretation (van der Klaauw, 1931 : 33). Of further interest in this regard is van der Klaauw's discussion of the false external auditory meatus, or meatus spurium, formed when the glenoid region is shifted posteriorly and abuts against the mastoid (or post-tympanic process) thus constituting a ventral bridge between the bulla and external auditory opening. Such a squamosal-mastoid arch is sometimes present in *Nycticebus* and similar occurrences may account

for some of the reports of expanded ectotympanics in Lorisiformes. The derivation of the bony external meatus in prosimians can be of several different kinds. In tupaioids (*Dendrogale*) an entotympanic meatus, in some lemurs and lorises a partial contribution from the squamosal (meatus spurius), and a true or tubular bony meatus, which in *Tarsius*, cercopithecoids and hominoids is derived from the ectotympanic. Comparison of forms such as *Loris* or *Nycticebus* with *Tarsius* or *Necrolemur* at once shows how different these two types of progressive prosimians are in this region.

Auditory bullae of several well-preserved specimens of *Megaladapis* in the British Museum (Natural History) and in the American Museum of Natural History show that this genus exhibits a partial meatus spurius, but most sutures between the bones involved are closed. The arcuate bony attachment for the tympanum in *Megaladapis* (A.M.N.H. 30024) lies high on the dorsal face of a rather large bullar cavity (near the promentorium) and from it a sheet of bone fans out dorsolaterally, apparently an ossified annulus membrane. In complete contrast with *Necrolemur* the internal free margin of the ectotympanic extends through the spurius meatus surrounding it. However at the margin of the auditory aperture lies a partially separate, rugose bony rim. This rim is presumably the outer end of an ectotympanic tube (see Lorenz, 1905 : 463). Whatever the exact relationships with surrounding bones are, and these are obscured by closure of sutures, the ectotympanic of *Megaladapis* has no resemblance to that of *Necrolemur*. In fact, the appearance of the auditory region seems about as different in these two genera as could be expected for two mammals referable to the same order. Nor does the morphology of this part of the skull suggest any special affinity between them.

Hürzeler's view, that the annulus and osseous meatus in *Megaladapis* and *Necrolemur* are similar, even if tenable, would hardly provide relevant information for the assignment of the latter to the Lemuroidea. Rather, it emphasizes an aberrant feature of *Megaladapis*, a form which (together with a few little-known allied genera) has long been known to exhibit many characters divergent from the remainder of Malagasy Primates (Hill 1953 : 655). On the basis of a single feature, the conformation of the tympanic annulus, it cannot, of course, be asserted that similarities in its make-up relate *Necrolemur* and *Tarsius*, any more than one can say that a tubular construction of this bone relates *Necrolemur* and *Megaladapis*. If it were not for the many other characters shared by *Necrolemur* and *Tarsius* (see Table I, p. 52) ectotympanic resemblances between any two of the three could be ascribed to parallelism. Two conclusions suggested by the relationships discussed above are : 1) that *Megaladapis* in the region of the external auditory meatus diverges from both living Lemuroidea and from *Necrolemur* and 2) that *Necrolemur* exhibits a tubular osseous meatus not unlike that to be expected for an Eocene member of the particular stock from which *Tarsius* arose (Text-fig. 1).

Compared with living and post-Eocene Primates the structure of the ectotympanic of *Necrolemur* is more "advanced" than in any other known prosimian except *Tarsius*. Of course, demonstration that the centre of ossification of the external auditory meatus in *Necrolemur* lies in an embryonic horseshoe-like ectotympanic is not possible for this fossil species. Such a ring-like structure does precede the

tubular conformation in *Tarsius*. Consequently in the latter, this manner of development justifies reference to the tubular structure as part of the ectotympanic. Although developmental history is not known for *Necrolemur*, there is certainly nothing in the conformation of the annulus of the known adults to prove that it did not arise much as in *Tarsius*.

The only other fossil prosimian known to have a tubular bony meatus is *Plesiadapis*. A skull of this primate recently described by Russell (1960 : 312-314) found near Cernay, in French continental late Paleocene beds, shows that this form has an extremely long osseous auditory meatus. Considering the very great differences between *Necrolemur* and *Plesiadapis* in the remainder of their cranial anatomy, the conclusion that this feature in common is due to parallelism seems almost unavoidable. Moreover, instead of standing out from the skull base, as in *Necrolemur* and *Tarsius*, the osseous meatus of *Plesiadapis* is sunk between the adjoining bones, as in *Galeopithecus*.

Entotympanic and entocarotid circulation.—Hürzeler (1948 : 29) was unable to find a suture between the petrosal and bulla in *Necrolemur* and implied that this ranked it definitely with Lemuroidea and not Tarsioida. However, van der Klaauw (1931 : 285) indicates that the bulla arises in the latter group in the same manner as in lemurs. The presence of a separate centre of ossification for the bulla in tupaiaoids is now well established, but in the remaining Prosimii it apparently always arises from the petrosal. Consequently, the absence of a suture between bulla and petrosal does not distinguish lemuriform from tarsiiform Primates, and is equivocal here. It is, perhaps, not accurate to speak of prosimians, other than tupaiaoids, as having an entotympanic, but van der Klaauw (1931) considers that the entotympanic, when continuous with the bulla has simply lost its independence as an ossification centre.

Gregory (1915 : 430) was able to deduce from the positions of the entrance and exit of the carotid artery on the bulla that *Necrolemur* resembled *Tarsius* and not other prosimians in entocarotid circulation. Hürzeler's illustrations (1948, figs. 30, 31) confirm Gregory's suggestion of tarsioid affinities, by showing that his posited course for the entocarotid was correct and that the stapedia branch is smaller than the promentory artery, as in *Tarsius*. In *Tupaia* and those lemurs in which the carotid enters the bulla the reverse is the case (see Saban, 1957, fig. 36). There are, of course, the expected differences (between the Eocene and the living tarsiids) in the exact route of the entocarotid artery but such distinctions in *Necrolemur* do not approximate the Lemuroidea to any appreciable degree.

The tarsioid characters of Necrolemur.—Table I lists those features shared by necrolemurines and *Tarsius*, particularly those not occurring or seen only sporadically in Recent and fossil Lemuriformes and Lorisiformes. The limitations of tabular expression prevent detailed citing of sources (and partial exceptions); other students have, and may again assess some of these characters differently. Although opinions vary as to individual features it does not seem possible to question any longer that the complex, or nexus, of shared osteological details in necrolemurines and tarsiines justifies their close taxonomic association. Particularly to the point in this regard are the remarks of Gregory (1920 : 193) on the amount of variability

in morphology allowable within a single mammalian family. Many cranial similarities between *Tarsius* and *Necrolemur* can be attributed to parallelism, but to explain all those listed (and others not amenable to tabular presentation) in this manner would be to assert the impossibility of distinguishing between real evolutionary affinities and parallelism. Such an agnostic attitude does not seem justified in this case. Moreover, in mammalian palaeontology it is almost always easier to produce an argument favouring separation of two given groups than it is to prove their valid

TABLE I. A COMPARISON OF LEMUROID AND TARSIOID CHARACTERS

CHARACTER	LEMUROIDS		TARSIOIDS
	LEMURIFORMES (Lemuridae and Adapidae)	LORISIFORMES	TARSIIFORMES (Tarsiinae, and Necrolemurinae)
1. Lower canine	shorter than upper or incisiform	incisiform	longer than upper
2. Zygomatic arches	typically stout (flaring)	variable (flaring)	slender (close to skull)
3. Postorbital opening (area)	large	rather large	almost closed or small
4. Brain case (transversely)	very narrow to expanded	expanded	much expanded
5. Muzzle (length)	long	long to medium	very short
6. Muzzle (width)	typically broad	variable	very narrow
7. Contact between jugal and lacrymal	typically occurs	often occurs	does not occur
8. Ectotympanic (position)	in bulla	at margin of bulla	extends out of bulla
9. Ectotympanic (shape)	annular	annular but broad	tubular
10. Elongation of calcaneum and astragalus	none	some	some
11. Inflation of bullae	typically inflated	little inflation	much inflation
12. Bony canal of promontory artery	small, in bulla	not ossified not in bulla	large, in bulla
13. Median lacerate foramen	variably present	present	not present
14. Carotid foramen	at posterolateral angle of bulla	not present	on ventromedial face of bulla
15. Septum between tympanic cavity and hypotympanic sinus	incomplete	complete	incomplete
16. Tibio-fibula	does not occur*		may occur in both subfamilies
17. Palate	broad anteriorly		narrow anteriorly
18. Tooth rows	parallel (U-shaped)		converge (V-shaped)
19. Upper canine	much larger than ant. incisor		smaller than ant. incisor
20. Molar hypocone	variable but often large		often small
21. Posterior nares (shape)	broad		narrow
22. Position, posterior nares	anterior to M ³		well behind M ³
23. Pterygoid alae	long anteroposteriorly		short anteroposteriorly
24. Bullae (position)	well separated		approximated anteriorly
25. Mastoid region	little or not inflated		inflated
26. Direction of foramen magnum	largely backward		largely downward
27. Posterior palatine torus	absent		present
28. Contact of external pterygoid alae with bulla	touching		broadly overlapping
29. Interfrontal suture	typically remains open in adults		fused in adults

* Characters following 15 are typical of both Lemuriformes and Lorisiformes.

association. Fortunately, in the case of *Necrolemur*, preservation of almost every part of the skull allows for more precise judgements of affinity than is usually possible for a fossil primate.

In summary, that *Necrolemur* stands close to *Tarsius* taxonomically is most strongly suggested by essential agreement in the following areas: entocarotid relationships within the bulla; shape and position of ectotympanic; position of the pterygoid wings and posterior nares; presence of a posterior palatine torus; likeness of relative sizes of teeth, tooth patterns, and arrangement of tooth rows; fusion of frontals, and many lesser features (Table I) which differentiate them from living and fossil lemuriform and loriform prosimians.

The post-cranial skeleton in necrolemurines.—Most features of the necrolemurine post-cranial skeleton reported to date need further confirmation. Schlosser (1907) assigned to *Microchoerus edwardsi* and *Necrolemur antiquus* (without association) several isolated limb-bones from the Quercy deposits. The calcanea figured by him resemble those of Primates, but there is always the possibility that the fused tibio-fibulae that he referred to *Necrolemur* actually belong to a rodent or insectivore. A fusion of this sort can occur in either order, and members of both occur in the Quercy phosphorites. The only valid association of post-cranial and cranial material in necrolemurines is reported by Weigelt (1933: 138). His specimen includes most of the bones of a left hind limb, found together with a skull and mandibles here assigned to *Nannopithecus* (p. 61). Weigelt claimed that the tibia and fibula were fused, but, on examination of the specimen, I can see no evidence for this. A small splinter of bone adjacent to the left tibia was regarded by him as a part of the fibula, but it does not contact the tibia. Also, the surface of the tibia is much worn and broken, has probably lost its original surface, and does not show any elevation for fibular attachment. Remaining parts of the pelvis and femur are not particularly like those of *Tarsius*, but the calcaneum, although broken, does show some elongation. If tibio-fibular fusion occurs in necrolemurines it has yet to be convincingly demonstrated. Moreover, it seems unlikely that the specializations of the hind limb of *Tarsius* should be expected to have been attained by any Eocene Primates. About all that can be said in defence of the possibility of such fusion is that in hopping prosimians like galagos and the tarsier the foramen magnum is directed almost downward, and since it also has this position in *Necrolemur* some such specialization of the hind limb might be expected.

Relationships.—The construction of the ectotympanic and the entocarotid circulation of *Necrolemur* are more like those of *Tarsius* than of any other known prosimian. Preservation of the bony canals of the promontory and stapedia arteries within the bulla of *Necrolemur* (Hürzeler, 1948, figs. 30, 31), shows that this form here resembles *Tarsius*, tupaoids, and Catarrhine Primates, but not lemurs or lorises (See Le Gros Clark, 1959: 151). In consideration of the many other similarities between these two genera, it seems advisable to rank the Necrolemurinae as a subfamily of the Tarsiidae. At present the case for associating the North American Anaptomorphidae (s.s.) with *Tarsius* is not nearly as sound, and rests largely on dental resemblances between necrolemurines and anaptomorphids. Only one partial skull (of *Tetonius*) is known for any of the numerous genera and species of North

American "tarsioids", and in it much of the basicranium is missing. Therefore, it is not particularly sound to refer to any of these New World species as tarsioids, although some of them may eventually prove to be so. At present, only the Necrolemurinae are demonstrably tarsioid.

For an early Tertiary primate *Necrolemur* is a progressive or advanced form, and in some features, such as the more complicated tooth patterns and more inflated mastoid region, less structurally primitive than *Tarsius*. Much of the overall morphology of the skull in *Necrolemur* is about as divergent from that of Eocene lemurs like *Adapis* and *Pronycticebus* as is that of the Recent tarsier. This progressiveness of necrolemurines, among Eocene prosimians, requires emphasis here because others have erroneously reported degrees of primitiveness not actually to be seen in known early Tertiary Primates, i.e. the supposed presence of three upper incisors and posterior palatine fenestrae in *Pseudoloris*. These two characters are exhibited by some Insectivora but not in Primates. Had they really occurred in *Pseudoloris* they would represent interesting morphological relics of the insectivore grade in primate ancestry, but actually *Pseudoloris* (and other necrolemurines as well) is as devoid of such features as are Recent Prosimii. In Primates antiquity is not always synonymous with primitiveness.

II. ASSIGNMENT OF *PSEUDOLORIS* TO THE NECROLEMURINAE

In 1890, Filhol described a small primate from the late Eocene phosphorites of Quercy, France, which he called *Necrolemur parvulus*. Later Stehlin (1916 : 1397) proposed a separate genus for this species, *Pseudoloris*, and pointed out a number of distinctions in the dentition separating it from *Necrolemur*. The validity of the genus *Pseudoloris* has been accepted in subsequent publications. Teilhard reviewed the species in 1921, basing his comments largely on new and more complete specimens. He disagreed with Stehlin's suggestion of an affinity between this Eocene primate and the living lorises, indicated in the generic name, and proposed that *Pseudoloris* not only had tarsioid affinities, but in some respects is more like the living *Tarsius* than any other Eocene primate. Simpson (1940 : 198) also considered the small Quercy primate particularly *Tarsius*-like and established for the one species *Pseudoloris parvulus* a separate subfamily, Pseudolorisinae, which he tentatively assigned to the Anaptomorphidae (*s.l.*) while remarking that "this genus stands considerably closer to *Tarsius* than does any other known from the Paleocene or Eocene, and should perhaps be placed definitely in the Tarsiidae". Simpson, however, did not list any characteristics of the subfamily. In the course of recent studies on European Eocene Primates the writer has concluded that it is not possible to place *Nannopithecus* and *Pseudoloris* in separate subfamilies. Since the former is clearly associated with *Necrolemur* in dental and cranial morphology and, through *Necrolemur*, with *Microchoerus*, it is advisable to formalize this association of four genera at the subfamily level. This subfamily has most often been called Necrolemurinae but the term Microchoerinae is also available. Due to greater currency and early establishment the former name is to be preferred.

Discussion.—Simpson did not specify why *Pseudoloris* should not be included in the Necrolemurinae, Teilhard having previously pointed out that among European

Primates, its closest resemblances are to species of *Necrolemur*. However, Simpson (1940: 199, footnote) observed that *Necrolemur* may have been derived from a paromomyine, and *Pseudoloris* from an omomyine source, and so indicated a separation in their lineages going back to the Paleocene. It is unlikely that *Necrolemur* could be derived from a paromomyine stem, because the anterior lower dentition is less reduced in number of teeth than in paromomyines (unless one assumes that the anterior enlarged tooth in *Necrolemur* is an incisor, see page 58). Even assuming that the teeth in question in *Necrolemur* are incisors, then the corresponding teeth in *Pseudoloris* are also most likely to be the same. In this regard these two genera stand together in the way in which they differ from, or, as is less probable, resemble the paromomyines.

In a point for point comparison of tooth shape and pattern in *Microchoerus*, *Necrolemur*, *Pseudoloris* and *Tarsius* it is evident that there is a greater similarity between species of the latter two groups, but this agreement may equally well be due to a relative lack of specialization in tooth patterns of both, as to a phyletic connection between them not involving the other genera.

Hürzeler's illustration (1948, fig. 4) shows that *Nannopithec* (at least in the characters of premolars and molars) approaches the dentition of *Tarsius* almost as closely as does that of *Pseudoloris*. Moreover, *Nannopithec* is certainly nearly related to *Necrolemur*, so that the Tarsiinae are linked by two separate types of intermediate dental morphologies with the Necrolemurinae.

That *Pseudoloris* has one or more small incisors anterior to the large lower tooth, here considered the canine (and thereby differed from other necrolemurines) has been repeated in the literature on this primate, for instance by Hill (1955: 313). Nevertheless, no teeth or alveoli have ever been observed in this position. The erroneous view that *Pseudoloris* possessed lower incisors seems to derive from Teilhard (1921: 6). However, in spite of suggesting that three upper incisors indicate the existence of lower incisors, Teilhard's final statement was neutral, being only (?) for lower incisors in the dental formula he gave. Specimens of *Pseudoloris* now in the Basel and Paris collections indicate that the alveolar border of the mandible (between the large anterior lower tooth and the symphyseal surface) is too thin to have supported a more anterior tooth. Moreover, this narrow band of bone never contains evidence of alveoli.

The partial facial region of *Pseudoloris* (Montauban C) from which Teilhard concluded that there are three upper incisors in this small primate, and the only specimen of the species which preserves alveoli here indicates that the existence of an I¹ should be strongly questioned. Considering the highly eroded surface of the premaxilla the tiny spot, visible only on the right side, which Teilhard interpreted as the alveolus of an I¹ could equally well be the result of post-mortem damage. For instance, erosion of the original alveolar margin may have exposed a matrix filled cavity in the bone. If an I¹ does exist in *Pseudoloris* it constitutes a more primitive condition than occurs elsewhere among all Primates, with the possible exception of *Nannopithec raabi* in which the evidence on this point is equivocal. Furthermore, if the presence of upper incisors calls for lower ones as well, then this assumption (to mention just a few cases) would apply equally to species of *Micro-*

choerus, *Nannopithecus*, and *Necrolemur*. Although the latter have two pairs of incisors above, most of the included species in these genera do not have teeth anterior to the enlarged lower tooth. The retention of P_1 in necrolemurines although P^1 is lost need not be anomalous because (unlike most Primates) members of this subfamily have rather small upper canines, which do not necessitate the formation of a diastema below for their reception. *Microchoerus ornatus* and *Pseudoloris parvulus* are at opposite extremes in this subfamily as regards dental patterns, but they are linked by a series of morphologically (not sequentially) intermediate species. If, as some authors have preferred, these genera are divided into three subfamilies, Microchoerinae–Necrolemurinae–Pseudolorisinae, the number of subfamilies approximates to the number of genera involved and completely conceals their essential similarities.

The proliferation of dental cuspsules and crenulations observed in the late Eocene species of *Necrolemur* and *Microchoerus*, but lacking in *Necrolemur zitteli*, and the species of *Nannopithecus* and *Pseudoloris* should not be given too much taxonomic weight. Complex molar patterns in *Microchoerus erinaceus* and *M. ornatus* particularly, were considered by some early authors as indicative of a separate subfamily or even family for *Microchoerus*. Nevertheless, such changes might be due to the spread of very few or even single gene alleles which, as the temporal succession of species in the European Eocene suggests, might have appeared and been selected for rapidly. Apart from this, necrolemurine species, including *Pseudoloris parvulus*, are so similar in general conformation of details of tooth structure, dental formula, shape of the horizontal ramus, jaw angle, depth of the mandible, and position of the primary mental foramen, that it is hard to avoid the conclusion that they belong to a distinct taxon of closely related species and genera.

Teilhard (1921) described and figured two large reniform fenestrae in the posterior palatal region of *Pseudoloris*. Such fenestrations do not occur in *Tarsius*, nor in other Primates, although some insectivores have openings here. However, in *Necrolemur* there is often an area just in front of the posterior palatine foramina where the palate is broken away. *Tarsius* also has a thin posterior palate, and in a much smaller and more delicate primate like *Pseudoloris* the probability that this part of the palatine should have been lost during fossilization or subsequent preparation is appreciable. Microscopic examination of the edges of these fenestrae shows no smooth margin but everywhere the rim of these holes is fractured and broken. Evidently these openings are not natural features but artifacts of preparation. They can no longer be considered significant diagnostic features of the genus.

Agreements between facial regions of the skull of *Pseudoloris* (Montauban C), of *Microchoerus* (Sedgwick Museum, Cambridge), and the more complete skulls of *Nannopithecus* (G.P.I.H. 4236) and of *Necrolemur* include the following relatively diagnostic tarsioid features: 1) comparatively large, anteriorly directed orbits; 2) reduction of snout size and length; 3) narrowing of the interorbital septum; 4) convergence of the tooth rows anteriorly; and in the latter two genera, at least, 5) fusion of frontals in the mid-line. These shared cranial features corroborate dental resemblances discussed on page 61.

To conclude, the similarities between *Pseudoloris* and remaining necrolemurines

are so great that it should be assigned to this subfamily. It may be noted that at one time or another one or more species of all the genera here included in the Necrolemurinae (*Necrolemur*, *Microchoerus*, *Nannopithecus*, *Pseudoloris*) have been assigned to the genus *Necrolemur*.

III. THE ANTERIOR TEETH OF *MICROCHOERUS* AND *TARSIVUS*

Interpretation of dental formulae in Primates.—For two principal reasons identification of the number and the kind of teeth in early Tertiary Primates is of basic importance in reconstructing primate evolutionary history. First, teeth are the most commonly preserved parts of these animals, and, second, once a tooth is lost from the series it cannot be reproduced again as such. From this latter it follows that species postulated to lie on or near the line of ancestry of a given form must have the same or a greater number of each kind of tooth than does a supposed descendant. An example is provided by the Paleocene and Eocene *Plesiadapis*. Latest known species of this genus have lost canines, first and second premolars (above and below) and a pair of lower incisors,—eight teeth in all. Since all living Primates, with the exception of the Madagascan Aye-Aye, *Daubentonia*, possess at least some of these teeth, *Plesiadapis* is thus eliminated from the near vicinity of any of their ancestral lines (and from that of *Daubentonia* on other, and very convincing, grounds; Simpson 1935). Huxley (1876) termed such forms (which cannot have given rise to later stages of a given group) *intercalary* types. From these, he distinguished *linear* forms, which in their structure admit of the possibility of being ancestral to subsequent groups, even when the lack of intermediate connecting links makes absolute demonstration of such ancestor-descendant relationships impossible (Le Gros Clark, 1959: 48). Although Huxley's terms have not received general acceptance they serve to emphasize the essential problem to be considered here,—whether the dental conformation in necrolemurines and tarsiines indicate *intercalary* or *linear* relationships between the two subfamilies.

A number of procedures, derived from comparative studies of all known forms govern the identification of teeth in Primates. Upper incisors in Primates, as in all mammals are always situated in the premaxilla. The upper canine, unless lost, is the most anterior maxillary tooth. When present, the lower canine is situated in front of the upper and shears against its anterior margin. Thus, the lower caniniform tooth in lemurs and lorises can be determined as the P_2 (despite a canine-like appearance), since its anterior edge shears against the posterior face of the upper canine. In these Prosimii the true canine has become incisiform and inclined forward, forming part of the tooth-comb apparatus. Apparently P_2 cannot shift forward so as to shear against the anterior face or blade of the upper canine and this makes it possible to distinguish P_2 from the canine in all cases. Identification of the anterior enlarged lower tooth in necrolemurines is not so simple, and the different assignments given this tooth have complicated discussion of possible relationships between the anterior lower teeth of necrolemurines and tarsiines.

For many years there have existed two conflicting interpretations of lower dental formula in Necrolemurinae, one affirmed by Stehlin (1916) for *Necrolemur* o.i.4.3., favoured by Hürzeler (1948) and by Hill (1955) and another presented by

Gregory (1915), 1.1.3.3., and avowed by Simpson (1937, and later). What has been obscured by this difference of opinion is that necrolemurines typically lack a tooth in front of the enlarged tooth and behind it have seven teeth. Consequently, no matter which of the alternative dental formulae is correct, all but one species of necrolemurines differ from, or resemble, *Tarsius* in the same way. This is not reflected by the taxonomic key for the group presented by Hill (1955 : 292) in which the procumbent anterior tooth is regarded as a canine in *Necrolemur* and *Nannopithecus* and as an incisor in *Microchoerus*.

Differences between anterior lower dental formulae in necrolemurines and *Tarsius* require elucidation in view of the cranial resemblance of both subfamilies. Moreover, the upper dental formulae of all species of both groups are apparently the same (2.1.3.3.), as are the sizes of the teeth relative to each other (which may be more important). For example, all tarsiids have an I² that is larger and longer than the upper canine.¹ This is the reverse of the condition in all notharctines, adapines, living lemurs and lorises, in which the upper canine is much larger and longer than I². A definite assignment as to type of the anterior tooth in the lower dental series of necrolemurines remains difficult. If it is unlikely, as Simpson (1937 : 146) remarked, that a lower canine can occlude in the position it does here, then it would appear that the lower enlarged tooth in all these European Eocene tarsioids, including *Pseudoloris*, is an incisor and that the lower canine is the reduced and premolariform tooth immediately behind it. Alternatively, the canine may be supposed to have been lost and four lower premolars retained. The presence of a small P₁ consistently in *Teilhardina*, situated somewhat to the outside of the midline of the tooth row (as in Necrolemurinae) seems significant here (in view of the other dental resemblances between *Teilhardina* and necrolemurines noted by Hürzeler, 1948). In *Teilhardina* the lower dental formula is 2.1.4.3. Because of this, it is no longer possible to say that there are no known tarsioids of the early Tertiary which retain four premolars (Simpson 1937 : 146). As Hürzeler noted the Necrolemurinae, on the basis of dental evidence, probably derive from an Old World omomyid like *Teilhardina* and represent a phylum in which progressive reduction of the lower incisors took place.

The criticism can be made that the assumption of total loss of lower incisors in typical necrolemurines has no known parallel among other Primates. This is correct, but the loss of all but a single lower pair of incisors is more common in Primates than has been previously stressed. Apart from *Tarsius* and one species of *Microchoerus* this condition also obtains in *Parapithecus*, in the adapine genera *Caenopithecus* and *Protoadapis*, perhaps in the notharctine *Pelycodus*, and in indrisines including *Indri* and *Propithecus*. Such rather broad distribution of lower incisor reduction among both living and fossil tarsioids and lemuroids indicates that parallelistic tendencies for tooth loss here are strong among Primates, and make the total loss of lower incisors in late necrolemurines appear more plausible than the assumption that the large lower anterior tooth is not a canine but an incisor, as in plesiadapids and *Phenacolemur*.

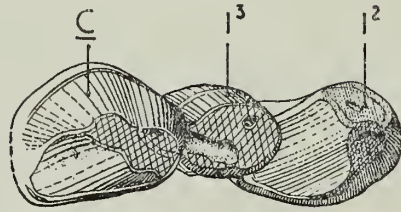
¹The most anterior upper incisor in necrolemurines is here arbitrarily considered I².

Should the enlarged anterior tooth be an incisor in Necrolemurinae then all members of this group stand distinctly apart from *Tarsius*, and it could not have descended from a species even distantly resembling necrolemurines in this regard. However, an alternative interpretation is suggested by specimens of *Microchoerus erinaceus* and *M. edwardsi* in the British Museum (Natural History) which is much more in agreement with the tarsier dental formula.

The British Museum specimens.—The lower dental formula of *Tarsius* is generally assumed to be 1.1.3.3. From front to back in the mandible these teeth are identified as, first, a small, pointed incisor, followed by a large and long canine, three premolars (increasing in size posteriorly), and three simply constructed molars, of which M_2 is the largest. In necrolemurines, on the other hand, the lower dental formula (assuming the anterior tooth is a C) is written 0.1.4.3. However, an exception to this formula apparently occurs in one necrolemurine species. Two specimens of *Microchoerus edwardsi* in the British Museum show a small alveolus anterior to the enlarged procumbent tooth, giving a lower dental formula of 1.1.4.3. This is further confirmed by a specimen of the same species in the Paris Museum (identified as Bach, lot 1893-11). Other necrolemurines do not show this small anterior alveolus. However such a possible identification of the lower dental formula of *Microchoerus edwardsi* (because that of *Tarsius* could be derived from it) indicates the need for a more certain assignment of the large procumbent lower tooth in necrolemurines. Some clarification of this point is provided by the following specimen of *Microchoerus* in the British Museum (Natural History).

The holotype of *Microchoerus erinaceus* Wood, B.M.N.H. 25229 (Text-fig. 2) includes the entire upper dentition (on one side or the other) and an associated mandible with P_3 - M_3 . The anterior half of this jaw (with all teeth) was part of the original find, by Wood (1846). Cooper (1910) noted that the anterior portion of this mandible had been lost. However, the series of specimens of *Microchoerus erinaceus* in the British Museum (Natural History) from the late Eocene deposits near Hordle, Hampshire and from various localities in the Isle of Wight is extensive and includes several isolated lower canines, and a number of anterior parts of mandibles with premolars. These specimens of *Microchoerus erinaceus* are also supplemented by a number of jaws and a fragmentary facial region from Hordle in the Sedgwick Museum, Cambridge. The occlusal diagram shown here (Text-fig. 2) is based on the holotype, supplemented by the others mentioned above and by Wood's figure.

The holotype has well-preserved wear facets on the three anterior upper teeth, I^2 , I^3 , and C. These surfaces of wear indicate that the tip of the lower canine could be extended anteriorly to occlude against I^2 , presumably when the animal was nibbling, but that when the jaws were shut its apex wore against I^3 and its base against the upper canine (see Text fig 13b). In *Tarsius*, the lower canine (which no one seems to doubt is a canine) can likewise occlude against these same three upper teeth. In *Tarsius* there is not the same degree of procumbency as in *Microchoerus*, so that wear on these three upper teeth in the living species, takes a rather different course. However, relative sizes of the teeth involved, and their general position in the jaw is similar in both genera, and upper dental formulae the same.

FIG.2A Upper right I^2 - C :

C - I^3 : Cross hatched—wear surface sloping postero-lingually made by lower canine when teeth are fully occluded.

I^2 : Cross hatched (fine) internal wear surface made by lower canine when nibbling

I^2 Dotted lines—external wear surface made when lower canines are swung laterally during nibbling.

FIG.2B Left anterior dentition (fully occluded).

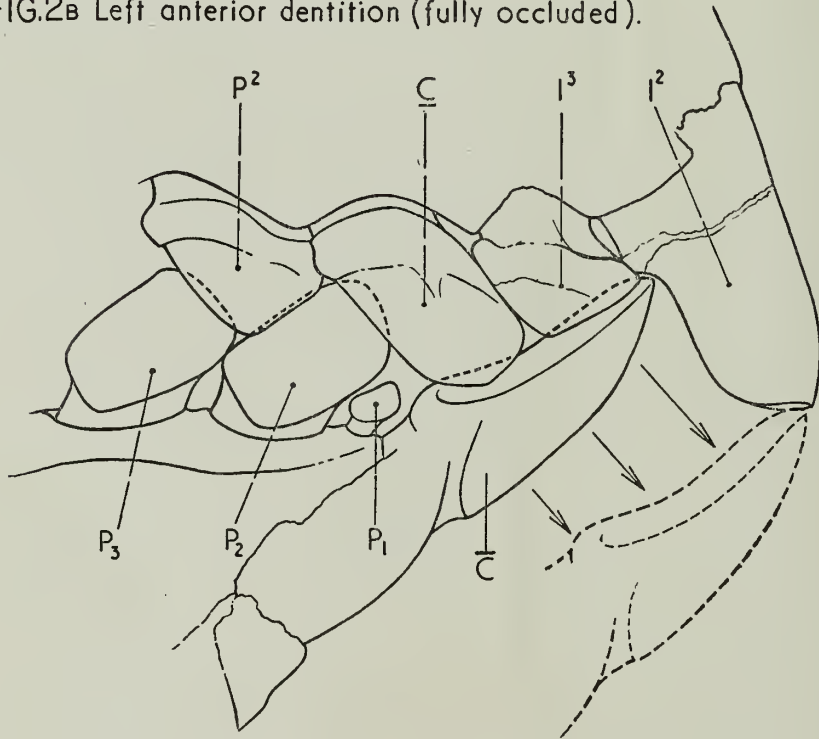


FIG. 2. *Microchoerus erinaceus* Wood. Diagrams of anterior wear pattern and occlusal relationships. (B.M.N.H. 25229).

A reasonable assumption would be that a generalized necrolemurine, with a lower dental formula identical to that of *Microchoerus edwardsi* could have given rise to that of *Tarsius*.¹ All that would be needed to achieve this is loss of P₁ (already non-functional in necrolemurines) and reduction of the degree of procumbency of the anterior lower teeth. If, in spite of the foregoing analysis, anyone still prefers the idea that the enlarged anterior tooth below (in this subfamily) is an incisor, then it would be equally logical to conclude that the large second tooth in the lower dentition of *Tarsius* is also an incisor. It is known that the P₂ in Primates can become caniniform, but apparently no one has yet suggested that incisors might do this also.

One reservation regarding lower dental formulae in this group should be made. Because of the great delicacy of the anterior alveolar border of the mandibles in these small mammals, and consequent breakage, it is difficult to be certain that they could not have had teeth anterior to the lower canine. Nevertheless, I have not found alveoli in this position except in *Microchoerus edwardsi*. Dental formulae in remaining necrolemurines may be written as follows:—

<i>Microchoerus erinaceus</i>	<i>Pseudoloris parvulus</i>
2.I.3.3.	2.I.3.3.
—	—
0.I.4.3.	0.I.4.3.
<i>Necrolemur antiquus</i>	<i>Nannopithecus raabi</i>
2.I.3.3.	2.I.3. (or 4). 3.
—	—
0.I.4.3.	0.I.4. 3.

As will be seen from the above formulae it is fairly certain that all four species have the same number and kind of teeth, identical with the living *Tarsius* above, but differing from the latter in lacking the single pair of lower incisors, and in possessing a vestigial P₁.

IV. REVISION OF *NANNOPITHECUS* AND ITS RELATIONSHIP TO OTHER NECROLEMURINES

Taxonomic position. An examination of the type of "*Pseudoloris abderhaldini*" Weigelt (1933) indicates conclusively that it is conspecific with "*Necrolemur*" *raabi* Heller (1930). The later species is referable to *Nannopithecus*. Weigelt was perplexed by the recovery of a skull different from *Necrolemur* (G.P.I.H. 4236) associated with lower jaws that were remarkably like those of "*Necrolemur*" *raabi*. These mandibles were illustrated by Weigelt (1933, pl. 4, figs. 2A, B), who quite correctly observed that this upper dentition could not belong to a species of *Necrolemur*. He therefore described the specimen as a new species of *Pseudoloris*. This assignment, although still not correct, was an improvement. In the vicinity of this

¹*Microchoerus edwardsi* appears to be disqualified as a direct forerunner of the tarsiers by possession of complexities in cheek tooth patterns not seen in *Tarsius*.

specimen were also collected elements of a left hind limb of a primate. These Weigelt believed could be assigned with high probability to the same individual as the skull (G.P.I.H. 4236). As such, they comprise the oldest partial skeleton of a tarsiid.

Published observations on the Geiselthal species of *Nannopithec* are somewhat confusing because of the early misidentification of the generic position of the Brown Coal species and it is necessary to outline the successive views held regarding it and closely allied forms. Simpson (1940 : 199) questioned the taxonomic placement of the "two" species and first suggested that evidence for a specific separation of "*Pseudoloris abderhaldini*" and "*Necrolemur*" *raabi* is dubious.

In an attempt to separate the two supposed species, Weigelt went to great lengths to set out some consistent differences in their mandibular dentitions. These distinctions are not convincing. It appears that the individuals called "*Necrolemur*" *raabi* are in most respects slightly larger and have a deeper horizontal ramus of the mandible than has "*Pseudoloris abderhaldini*". There does not seem to be any distinction between the two "types" that could not be due to sexual dimorphism or to population variation within one species. The partial skeleton of "*Pseudoloris abderhaldini*" was recovered from the Leonhardt Mine locality, while all the individuals of "*Necrolemur*" *raabi* appear to be from the Cecilie Mine. It is unlikely that the fossil-bearing strata in the two mines are of exactly the same age, but no appreciable time interval can be assumed.

Not knowing the upper dentition, Heller (1930) had some basis for placing "*Necrolemur*" *raabi* in the genus *Necrolemur*, even though later evidence proves this determination to be wrong. His assignment was plausible at that time because of the strong similarity in lower tooth structure between the German form and some of the less specialized necrolemurines such as "*Necrolemur*" *filholi*. In defence of Weigelt's placement of the species he described, it can be said that the upper dentition of "*Pseudoloris abderhaldini*" is superficially like that of *Pseudoloris parvulus*. This is mainly because, in dental patterns, they are both of a rather generalized tarsiid type. However, this similarity is not profound, and the lower dentitions of the two species are quite different.

Hürzeler (1948) tentatively equates *Necrolemur filholi* Chantre & Gaillard (1897) with *Nannopithec pollicaris* Stehlin (1912). He appears to hesitate somewhat on the question of whether or not to retain the genus *Nannopithec* for this form, but the identity of the two species seems to be beyond question. Although *Nannopithec filholi* has much simpler cusp patterns than *Necrolemur antiquus* the two are linked morphologically by *Necrolemur zitteli*, as is convincingly demonstrated by Hürzeler (1948).

Hürzeler's elucidation of the dental characters of *Nannopithec filholi* has provided the key to the correct assignment of the Brown Coal necrolemurine. Comparisons of the two species indicate that they are congeneric. The evidence (given below) for a specific distinction between them is not extensive, but at present it seems better to retain *raabi* for the Geiselthal form. Both species of *Nannopithec* appear to be of early Middle Eocene age. Faunal correlations indicate that species of this genus occur in Lower or Middle Lutetian deposits. At present, specimens of *Nannopithec*

have been recovered near Egerkingen in Switzerland, at Buchweiler in Alsace, and in the Geisel valley near Halle, Germany. *Nannopithec* does not occur in the Quercy

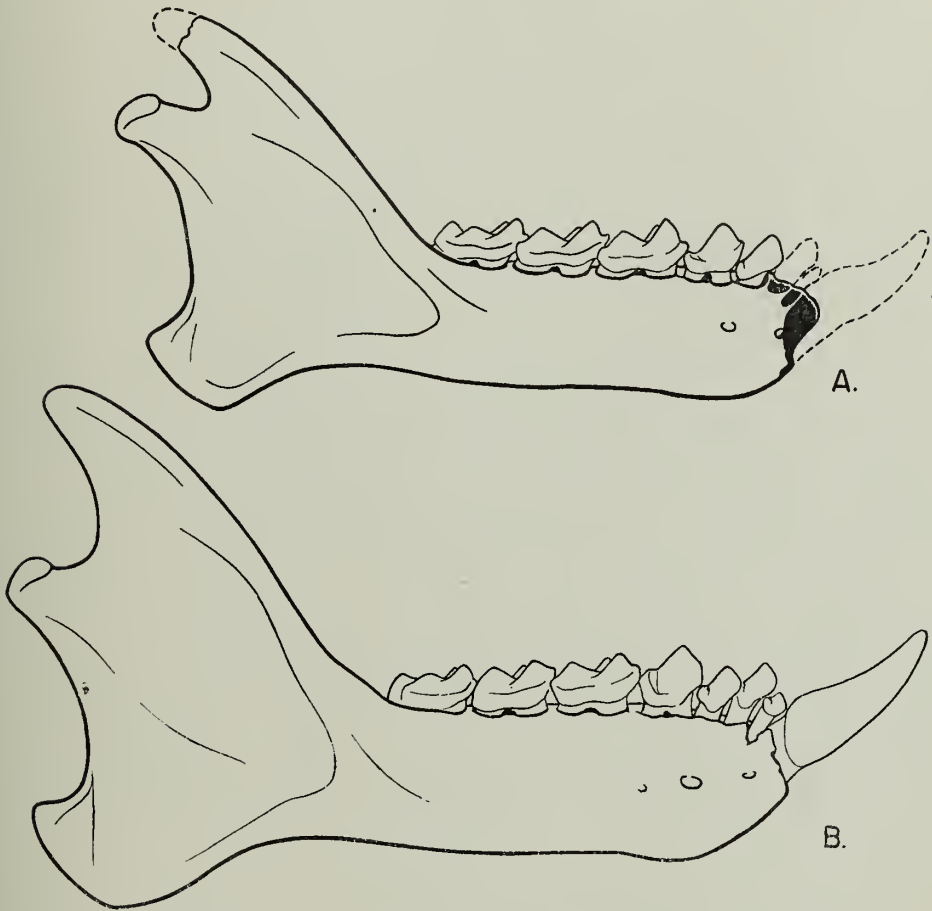


FIG. 3. A. *Pseudoloris parvulus*, based on mandibles in the Paris Museum, $\times 8$ approx.

B. *Nannopithec raabi*, based on specimens at the Geological and Paleontological Institute of Halle University, particularly G.P.I.H. 4254 and 4255 $\times 8$ approx.

phosphorites of Bartonian and Ludian age. Its absence at this later period reinforces the idea based on morphology that a species of this genus could have given rise to *Necrolemur*.

Genus **NANNOPITHEX** Stehlin, 1916

TYPE SPECIES.—*Nannopithecus polycaris* Stehlin, (= *Necrolemur filholi* Chantre & Gaillard).

2.1.3. (or 4). 3.

GENERIC CHARACTERS.—Upper M differs from that of *Pseudoloris*

0.1. 4. 3.

in presence of nannopithecus-fold running from posterior crest of protocone toward hypocone. Hypocone of M¹ comparatively smaller than in *Pseudoloris*; external median indentation between paracone and metacone of M¹⁻³ less pronounced, and metacones of M¹⁻³ relatively smaller and lower than in *Pseudoloris*; all teeth with some crenulation of enamel suggestive of teeth of *Necrolemur* but unlike those of *Pseudoloris*. P₄, compared to lower molars, much larger, and molar cusps more rounded and less high than in *Pseudoloris*; molar paraconids more distinct than in *Pseudoloris*; M₃ entoconid and hypoconulid not as high or as sharply set off as in *Pseudoloris*. (Known species slightly smaller than *Tarsius spectrum* or *Necrolemur zitteli*, somewhat larger than *Pseudoloris parvulus*.)

DISCUSSION.—Considering that *Pseudoloris* and *Nannopithecus* possess very simple and unspecialized dental patterns the differences between them are marked, being about as great as those which separate either from the living *Tarsius*. However, both show distinct affinities with *Necrolemur* and with *Microchoerus* as well as with *Tarsius*. Insofar as dental characters go (and osteological features do not contradict them) no basis whatever remains for placing these five genera in several different families and sub-families, as has been done in the past.

The skull of *Nannopithecus raabi* from Halle retains the entire upper dental series on one side or the other (except the canines) and this indicates the dental formula given above. Weigelt (1933 : 129) suggested an upper dental formula of 2.? .3.3. for the Geiseltal species, but his discussion, figures, and (much better) the specimen itself, indicate another possibility, 2.1.4.3., (Weigelt, 1933, pl. 5, figs. 1, 4, 5) for the upper dentition of *Nannopithecus raabi* (G.P.I.H. 4236). This photograph shows that the most anterior tooth preserved in position is much smaller than that just posterior to it which is clearly P². Although there is some breakage in the specimen, microscopic examination confirms that the seven teeth of the upper left side are an unbroken series. The four anterior teeth make up a sequence increasing in size posteriorly, and (considering what is known of the anterior upper teeth in *Microchoerus* and *Necrolemur*, and of these teeth in European Eocene Primates generally) they can hardly be other than the series P¹⁻⁴. Such an assumption is particularly necessary, if, as Hürzeler has suggested, a species of *Nannopithecus* is to be considered ancestral to *Necrolemur antiquus*. Otherwise, it is required to assume that in the line leading through *Nannopithecus* to *Necrolemur* the upper canine was first reduced (from a primitive large size, presumed characteristic of ancestral Primates) to a size smaller than the P² and subsequent to this re-acquired a size larger than that which the P² has in *Pseudoloris*, *Microchoerus* and (as is more important) in *Necrolemur*. It is more likely, therefore, that the canines have been lost from this specimen. Weigelt is apparently correct in his identification of the two loose teeth found in the region of the anterior extremity of this skull. The larger and most anterior tooth

he considered I², a smaller one I³. These teeth resemble I²⁻³ of *Microchoerus*. Should the dental series be complete in G.P.I.H. 4236 then the smaller tooth anterior to the P² would have to be considered a canine, and the D. F. would be 2.1.3.3. above, as in *Microchoerus* and *Necrolemur*. Even so, this is a different formula from that given by Weigelt which is one tooth short by his own account. The presence of a small upper P¹ would correlate well with the dental formula expected for a necrolemurine ancestor.

NANNOPITHEX RAABI (Heller)

(Text-figure 3)

1930. *Necrolemur raabi* Heller, p. 35, pl. 5, figs. 5, 6.

1933. *Pseudolovis abderhaldini* Weigelt, p. 128, pl. 3, fig. 5; pl. 4, figs. 1-3; pl. 5, figs. 1-5; pl. 9, figs. 4, 5; text-figs. 1-3.

MATERIAL.—G.P.I.H. 4254-4257, mandibles, and G.P.I.H. 4236, skull, with associated mandibles and hind limb.

HORIZON AND LOCALITY.—Geiseltal Brown Coals, Middle Eocene; near Halle am Saale, Germany,—from Leonhardt and Cecilie mines.

DIAGNOSIS.—Size: about as in *Nannopithec filholi* or slightly larger. Protocones of P³⁻⁴ somewhat more distinctly set off than in *Nannopithec filholi*, P² slightly longer antero-posteriorly than in the latter species; nannopithec-fold on M² less distinct than in *Nannopithec filholi*. Mandible: M³ hypoconulid slightly more distinct than in most specimens of *Nannopithec filholi* but enamel crenulations not as pronounced as in latter.

Discussion.—The lower teeth of *Nannopithec raabi* approach more closely the dentition of *Nannopithec filholi* from Buchweiler, in Alsace at Basel, Bchs. 647, than they do the specimen from Egerkingen, Basel Eh. 601,—particularly in the conformation of the M₃ talonid. Otherwise, except for the characters mentioned in the diagnosis above, the dentitions of the various specimens of *Nannopithec* illustrated by Hürzeler (1948) are not very distinct from the Geiseltal specimens. Pending a better understanding of faunal correlations and, as long as so few really complete individuals are known, it seems better to retain two species for the genus *Nannopithec*.

Perhaps the greatest significance of the Geiseltal finds of *Nannopithec* is the information supplied regarding early primate anatomy by the comparatively complete skull, mandibles, and hind limb found there. These remains make up the oldest known partial skeleton of an Old World primate. As a consequence of their significance, these remains were discussed in some detail by Weigelt, and will not be repeated here. There are, however, a few further comments of value to be made about the specimen.

Although the skull is crushed, it is evident that the orbits in this primate were very large. Most of the posterior wall of the orbit can be seen on the left side and it stretches from the lateral extremity of the skull to the mid-line (Weigelt, 1933, pl. 3, fig. 1). On the left side of the dorsal surface of the frontal the supraorbital margin and the juncture with the zygomatic arch is preserved. This region is very similar

in appearance to the corresponding area of *Necrolemur* skulls and, as in the latter, the interfrontal suture appears to be closed. Most of the characters of the basicranium are indeterminate, but in the region of the left external auditory meatus are numerous fragments of cancellous bone, which are presumably remnants of air cells of an inflated mastoid region, as in *Necrolemur*. The appearance of the detached back of the palate also agrees with that of *Necrolemur antiquus*.

As already mentioned (p. 53) the hind limb figured by Weigelt provides no evidence that this primate had distal fusion of tibia and fibula, which is commonly supposed to be the case in *Necrolemurinae*. Simpson (1940: 196) expressed the opinion that there is a general resemblance between the hind limb of the Geiseltal tarsiod and that of *Hemiacodon*, insofar as he was able to determine without seeing the originals. Examination indicates that, as he then suggested, most of the features of difference from *Hemiacodon* apparent in the Halle specimen seem to be the result of crushing.

MEASUREMENTS (in. mm.) *NANNOPITHEX RAABI*

(Specimens at the Geological and Paleontological Institute of the Martin-Luther University of Halle-Wittenberg, Halle-am-Saale, Germany). G.P.I.H. 4236, Leonhardt Mine, holotype of "*Pseudoloris abderhaldini*".

Maxilla :	Anteroposterior diameter	Transverse diameter
P ¹	1.1	0.7
P ²	1.8	1.1
P ³	1.7	2.0
P ⁴	1.5	2.3
M ¹	1.9	2.5
M ²	1.8	2.7
M ³	1.4	2.2

Anteroposterior diameter p¹ through M³,—10.1 mm. G.P.I.H. 4255, Cecilie Mine.
Mandible :—

Anteroposterior diameter \bar{C} through M₃,—11.7 mm.

Anteroposterior diameter \bar{C} through P₄,—6.8 mm.

Anteroposterior diameter M₁ through M₃,—4.9 mm.

NANNOPITHEX FILHOLI (Chantre & Gaillard)

DISCUSSION.—Inasmuch as the studies undertaken by the writer are in agreement with Hürzeler's tentative equation of *Nannopithecus pollicaris* and *Necrolemur filholi* this species takes the name *Nannopithecus filholi*, as discussed above. Hürzeler (1948) figured and reviewed amply all known materials of this species. Consequently, it will not be re-diagnosed here. One possible difference between Stehlin's type species and the mandibles described by Chantre & Gaillard is that the P₄ of the former

specimen does not have the roots as well separated as in typical *Nannopithec*. However, this character is variable in individual specimens of *Necrolemur*, and may not have much taxonomic value.

V. CONCLUSIONS

The findings reported here substantiate the position that tarsioids can be distinguished from lemuroids as far back as the Middle Eocene. Neither the Middle Eocene *Nannopithec*, nor the better-known genus *Necrolemur* provide any anatomical basis for a horizontal grouping of the Necrolemurinae with contemporary Eocene lemuroid Primates. Consequently, the Necrolemurinae have been ranked under the Tarsiidae.

Tarsioid claims for any other early Tertiary primate stocks are hard to support on the basis of present evidence. Some or all of the forms now ranked in the Omomyidae and Anaptomorphidae, may eventually prove to be so (with the advent of new and better specimens), but demonstrating tarsioid characters—ultimately derived from the living genus—becomes increasingly difficult with greater antiquity. Because of this it is possible that the direct ancestry of the Necrolemurinae might not have been definable as tarsioids much before the early Eocene.

Probably *Teilhardina*, an *Omomys*-like primate from the Belgian early Eocene (Sparnacian), bears a relationship to the stock from which the necrolemurines arose, and it in turn suggests an omomyid derivation for these tarsioids. A complex of characters including large anterior lower teeth, a tendency toward reduction of tooth number, frequent occurrence of a large $P\frac{4}{4}$ (non-molarized), nannopithec-fold and a number of other features suggests that the anaptomorphids (s.s.) are also a closely related stock. The current narrowly drawn higher categories of Paleocene and Eocene primates tend to obscure broad synthetic similarities among a number of stocks, but without better material there is little basis for grouping together any of such currently proposed early Tertiary primate families as Adapidae, Omomyidae, Anaptomorphidae, Paromomyidae (including Phenacolemurinae), and Tarsiidae (including Necrolemurinae).

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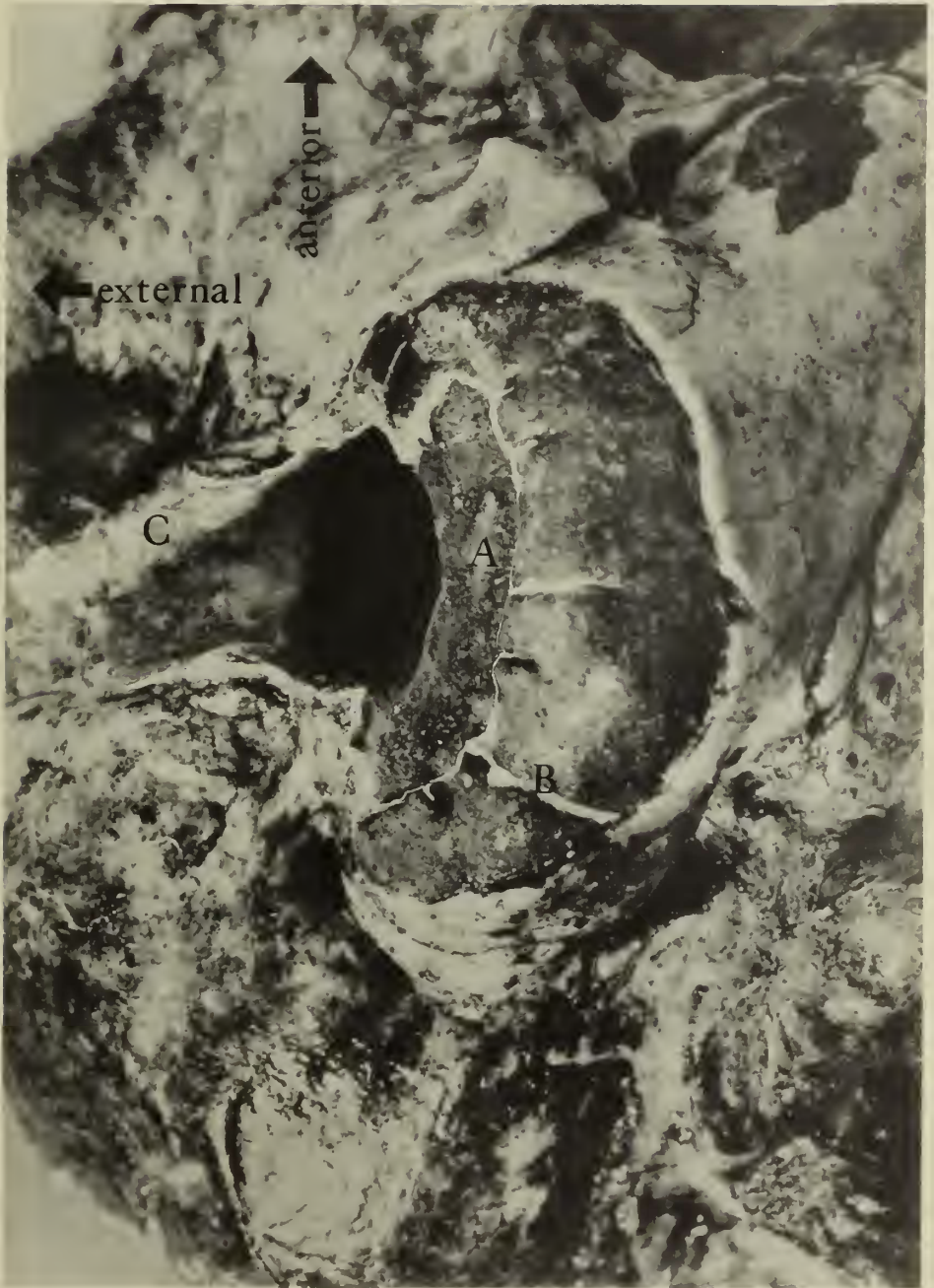
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PLATE 12

Necrolemur antiquus Filhol.

Ventral view of right auditory bulla, slightly retouched. A, region of ectotympanic and ventral bulla wall. B, strut between bulla and internal margin of ectotympanic. C, part of tubular osseous meatus. $\times 10$. (B.M.N.H. M 4490).



NECROLEMUR

PLATE 13

Necrolemur antiquus Filhol.

Internal view of part of the ventral wall of the right auditory bulla, showing expanded ectotympanic fused to bulla by struts (A) and continuous with broken osseous meatus at (B). × 20. (B.M.N.H. M 4490).

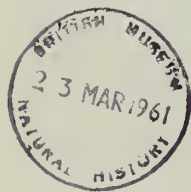


NECROLEMUR

PLATE 14

Adapis parisiensis Blainville.

Auditory bulla, left side (with ventral wall removed), showing free annular ectotympanic within the bulla at A. $\times 5$ approx. (B.M.N.H. M 1345).





ADAPIS